THE GREAT GLASS-SPONGE COLONIES OF THE DEVONIAN; THEIR ORIGIN, RISE, AND DISAPPEARANCE

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A very striking feature of the biota of the Devonian as represented in the state of New York is the extraordinary development in its late stage, the Chemung period, of its silicious hexactinellid sponges. At various levels in the sandy deposits of this time they are found, sometimes as scattered individuals and sometimes in plantations of uncounted numbers, so that it is safe to say that from the bottom of the formation in the "southern tier" of counties to near its summit, the hexactinellids of this order, the Dictyospongida, are many times more abundantly represented than in all the rest of the world together. In their extensive monograph of these sponges Hall and Clarke ascribe seventy-seven species in sixteen genera to this formation within the borders of New York and the same rocks in northern Pennsylvania. Clarke has described a number of additional Chemung species, so that there are now about ninety outstanding specific designations for this Devonian assemblage.

Sometime it will be a subject for discussion among morphologists whether this so-called order, Dictyospongida, is homogeneously constituted; probably it is not, but so seldom is the spicular structure retained in the sandy matrix that on the basis of general form and habit, and the arrangement of the spicular bands which are usually sharply preserved in impressions, all the sponge occurrences in this formation and those of like composition in the Mississippian faunas of Ohio and Indiana are now for convenience put in this single group. That they are for the most part accurately referred to the hexactinellids is abundantly shown by the spicular structure of the Mississippian species which has been demonstrated. The described species and genera have been established with the best

knowledge available; more exact determinations must await better preserved materials.

AREA OF OCCURRENCE

The area of deposition in which these Devonian hexactinellids are most prolific is quite distinctly limited along the line of outcrop in the region running from Cattaraugus County on the west to Otsego County on the east, about 150 miles; they accompany the area of most typical sandy sediment. As soon as the formation begins to lose in sand in its extension westward and to the east the sponges disappear.

NUMBER AND NATURE OF COLONIES

While scattered individuals and groups of sponges occur at random through these rocks and add much to the variety of the fauna, it is the great plantations or colonies that are here the subject of special reference. It is probable that we know as yet but few of the colonies that once existed. Some have been irreparably lost and doubtless others await discovery. But we may here take note of the following:

1. *The Hamlin Farm Colony*, Naples, Ontario County.—This lies nearest the base of the formation and is the oldest of all the colonies known. It appears to have been entirely composed of the species *Hydnoceras tuberosum* Conrad, of the tuberous or "alligator tail" type. Some hundreds of specimens have been found here.

2. *The Brown Hill Colony*, near Avoca, Steuben County.—Here again *Hydnoceras tuberosum*, the type of the genus and the first of all the dictyosponges to be described, is the prevailing if not the exclusive form. Wagonloads of these sponges have been taken from this place.

3. *The Jenks Quarry Colony*, near Bath, Steuben County.—The sponges here are also of the tuberous type but belong to the species *H. bathense*, H. & C., with an occasional representative of *H. botroedema* H. & C. This is the largest of all the assemblages. Workmen in the quarry, 30 years ago, found a layer of sandstone with a "curly grain" running through it that made it unfit for their

market and it was thrown out on the spoil bank. The discarded blocks came to the attention of the state's geologists and a carload of the layer was specially quarried for them. One slab of this layer, 8′×4′, now exposed in the State Museum, carries about 250 sponges lying as they were left, knocked over on their sides by some heavy tide. The carload of sponges contained probably not less than 5,000 individuals. The layer carrying them extended over the full face of the quarry, 120 feet, and indefinitely inward. The census of the colony cannot be estimated except in very large figures of tens of thousands.

4. *The Irish Hill Colony*, near Bath.—This is known only by the multitude of specimens of *H. botroedema* found loose in the soil at this place.

5. *The Halli Colony at Wellsville*, Allegany County.—Here the horizon is high in the formation and the species is *Thysanodictya Edwin-Halli* H., of which several hundred specimens were found by the late E. B. Hall, of Wellsville.

PREVIOUS HISTORY OF THE DICTYOSPONGIDA

Limiting the term to the characteristic expressions of the Devonian and Mississippian, they have little record of previous history; there is a single doubtful specimen from the mud beds of the Hamilton shales (*Clathrospongia? hamiltonensis* Hall) and some hexactin patches in the black Marcellus shale, *D.? marcellia* Clarke. Fragments of like type, but heretofore unrecorded, have been found in the Rochester shale of New York. In this statement we are eliminating from the group the Cyathospongia forms of the Utica shale, the Levis beds of Little Metis (Ordovician), and the extensive assemblage of similar hexactinellids in the Cambrian, especially those found by Walcott but not yet described. It is proper to exclude these even though they may have full ordinal relation with the Devonian species, because of the vast vacant interval of time between the earlier and later records. There were species of these sponges in the upper beds of the Portage group (three of Hydnoceras, one of Prismodictya, one of Dictyospongia, and one of Clepsydrospongia), but they must be regarded as

belonging to the advance guard of the Chemung army, as in various respects the faunal relations of the two are close.

HABITAT OF THE DEVONIAN SPONGES

These glass sponges obviously grew on sandy bottom at a depth which could not well have been more than one hundred fathoms, and probably not more than fifty. The waters of the epicontinental seas were always shallow; even the clay and lime muds betoken no depth comparable to the deep-sea oozes and blue muds of the present oceans. There is no single exception to this interpretation that could carry any weight in the presence of such overwhelming proof of the adaptation of this great array to conditions of life wholly unlike those under which their successors are living. When the Devonian time was over the simpler and typical expressions of the obconical, prismatic, and nodose sponges disappeared and were replaced by accelerated species of like stock (twenty species are recorded by Hall and Clarke) in the Mississippian stage, the Waverly and Keokuk divisions, in which there is a notable increase of lime sedimentation and consequent evidence of a deepening sea.

HABITAT OF LIVING HEXACTINELLIDS

Depth habitat.—Generally and specifically, these are deep-sea animals. Agassiz dredged them from 2,410 fathoms, but the "Challenger" expedition, as shown in Schulze's report, determined a greater range and a greater depth. The "Challenger" garnered about one hundred species, none of which grew at less than ninety-five fathoms. The summary of the record is as follows:

From	95 to	200 fathoms	24 species
	200 to	300 fathoms	none
	301 to	700 fathoms	35 species
	701 to	900 fathoms	none
	901 to	1,000 fathoms	2 species
	1,001 to	2,900 fathoms	47 species

Thus all the species are of the deeps and many of the very great depths.

Ground habitat.—The nature of the ground determined for 101 of these species is given by Schulze as follows:

Material	Number of Species
Sand	5
Gravel and stones	2
Hard ground	6
Coral mud	7
Volcanic mud	14
Green mud	1
Red mud	2
Mud (including blue mud)	32
Red clay	11
Globigerina ooze	13
Pteropod ooze	7
Radiolarian ooze	2
Diatom ooze	9

Schulze observes that forms equipped with root tufts were principally found in soft muddy ground, and in the Devonian seas the species generally were provided with a more or less conspicuous tuft of this kind.

Temperature habitat.—The temperature of the Chemung period was probably pretty cool. Glacial ice had formed over the elevated land of the middle Devonian on the Atlantic border of this continent and now with partial resubmergence the refrigerated waters were discharging themselves, with abundant landwash, into the shallow seas. In the Portage division of the late Devonian an immigrating warm water fauna (the *Manticoceras intumescens* fauna) coming in from the west was blocked and stopped on its way, driven out or destroyed by the presence of the cool waters carrying the Chemung fauna.

Today the hexactinellids show an apparently different temperature control, as witness the "Challenger's" record:

North Temperate zone	20 species
Tropics	45 species
South Temperate zone	35 species

This apparent difference is compensated by the cold of the deep waters.

RELATIVE ABUNDANCE OF LIVING AND DEVONIAN SPECIES

Continuing to use the "Challenger" reports we find a contrast in the abundance of individuals growing in any one place, but in making this comparison we must remember that the zoölogist is dipping into the sea bottom with a rake on the end of a string, while the paleontologist is on the sea bottom itself, with dynamite, crowbar, and hammer. The "Challenger's" dredgings rarely found any considerable number of individuals at any one place; "generally only one or two specimens of each species were obtained at the same locality. Sometimes, however, a considerable number of specimens were found at once." None of this evidence seems to point toward colonies or plantations in such vast numbers as in the Devonian. Today the strongholds of the hexactinellids are about the Philippines, Little Ki and Kermadoc islands; in the deeps of the southern Indian Ocean between Prince Edward and Crozet islands; and in Atlantic waters, off the Bermudas and St. Thomas.

ONTOGENY OF THE DEVONIAN SPONGES AS AN INDEX OF THEIR ADVANCED AGE AND SPECIALIZATION

There are four simple types of morphology, contemporaneous and combined, among the Devonian dictyosponges: (1) the smooth obcone, regularly expanding like a cornucopia and gently contracting about the open aperture; (2) a six-sided prismatic or banana shape; (3) a subprismatic obcone with successive transverse rows of tufted nodes, typically eight to a row; (4) long obcones with concentric rings, like the horn of an Oryx. These simple expressions have a successive value in ontogeny.

The first group constitutes the genus *Dictyospongia*. The second, in its typical expression, is the genus *Prismodictya;* but in several species not included in that genus the prismatic phase is superinduced upon and subsequent to the smooth phase. In other genera or species the later growth of the prism may show a tendency to develop nodes at the prism angles. *Hydnoceras* is the name applied to the typical tuberous or nodose forms and *Ceratodictya* expresses the annulated phase. These different expressions are, as just observed, essentially successive in the chronologic order of

ontogeny. In a progressed species the preliminary phases may be reduced by acceleration and even suppression but they are usually determinable; that is, a species of Hydnoceras (cf. *H. Walcotti*

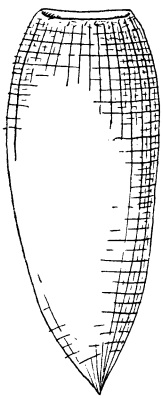


FIG. 1

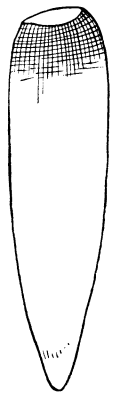
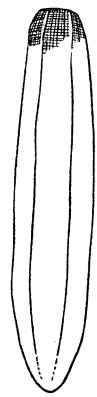


FIG. 2

FIG. 3



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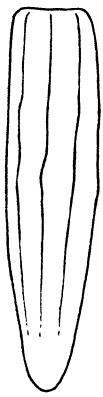

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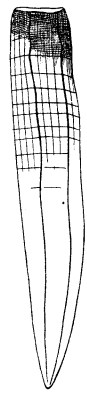


FIG. 6

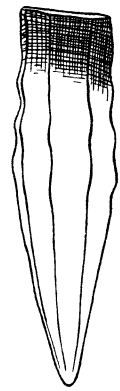


FIG. 7

FIGS. 1–3.—The typical or radicle form as expressed by (1) Cyathodictya and (2, 3) Dicyospongia.

FIG. 4.—The development of the Prismodictya faces.

FIGS. 5–7.—The Prismodictya type with inception of Hydnoceras tufts.

Clarke) will show over its initial surface, first the smooth and then the prismatic and tufted development, and even in its mature and final expression, decided development of the concentric rings.

These features of ontogeny are brought out for a number of species in the accompanying figures.

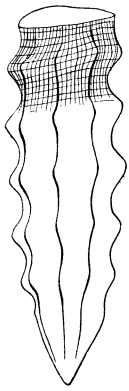


FIG. 8

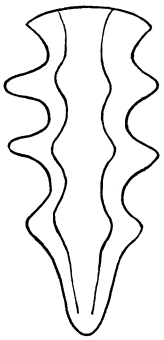


FIG. 9

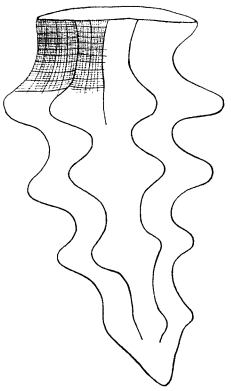
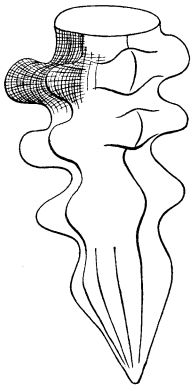


FIG. 10



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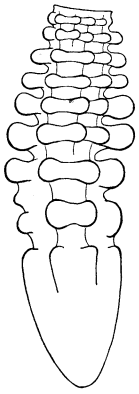

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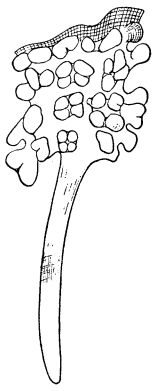


FIG. 13

FIGS. 8–11.—Various expressions of the Hydnoceras tufted type in which the Prismodictya and the earlier Dictyospongia stages are indicated.

FIG. 12.—Hydnoceras Walcotti; an extreme expression of this combination, showing notable retention of the Dictyospongia stage, union of the prismatic and tufted stages, and the development of the annulated condition.

FIG. 13.—Botryodictya, a condition in which the Dictyospongia stage is protracted and abruptly develops into a cup-shaped, tufted, and pouched condition.

In many species ontogenetic development is carried into extremes of nodosity and annulation, resulting, especially in later species, in great variability of form even within the confines of the Devonian.

Enough however has been given to indicate the degree of morphologic specialization displayed by these hexactinellids in the

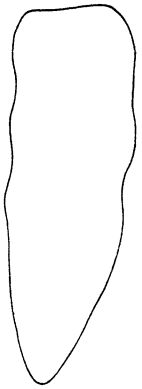
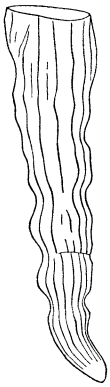


FIG. 14



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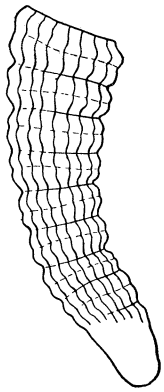

FIG. 16

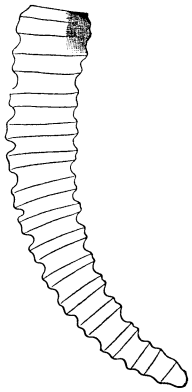

FIG. 17

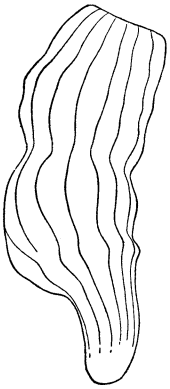

FIG. 18

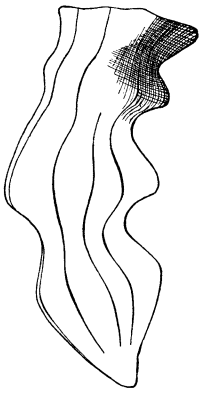

FIG. 19

FIG. 14.—The incipient annulated or Ceratodictya stage.

FIG. 15.—The annulated stage combined with an extreme expression of the prismatic form (Rhabdosispongia).

FIGS. 16, 17.—Phases of the Ceratodictya stage, Hydnocerina (16), showing departure from the type.

FIGS. 18, 19.—Expressions of two of these phases (Rhabdosispongia and Hydnoceras) from the Frasnian formation of France.

Devonian, a condition which must have required ages of time to work out. The Devonian sponge colonies must therefore have had a vast ancestry.

WHERE DO THESE DEVONIAN SPONGES COME FROM AND WHAT WAS THEIR ANCESTRY?

The answer to the first query may take this form: Between the species in the dark shale of the early Ordovician (Levis shales) and this invasion in the late Devonian, there is but a single recorded species which would seem safely placed among the Dictyosponges, viz., *Dictyospongia danbyi* McCoy from the Upper Ludlow (Silurian) of Westmoreland. We have referred to a similar occurrence in the Silurian of New York. It is quite possible that these were but derelicts tossed shoreward. The striking hexactinellids described by Dawson from the Levis shales seem to have for the most part the simple obconical foundation with special developments of spicular tufts which indicate that up to this time there had been no wide departure from the simple type of *Cyathospongia* which is repeated in the genus *Dictyospongia*. The other differentials of the Dictyospongida do not appear.[1]

The dark shales in which those early species (Ordovician and Cambrian) are preserved indicate a greater depth of water than do the Devonian colonies. We may therefore think of them as having invaded the deeper epicontinental seas from the much deeper waters of the continental edge at a time when the way was freely open to the margins of the platform. If they were traveling in toward ever-shallowing water there would or should be remains of them in the black shales and the sands of the interval deposits. There are none, and the fact constrains us to think that, instead of traveling into shallow waters, they were moving back to the deeper waters, where, concealed from the accessible rock records, they were working out their evolution. Then some impulse which may not be defined[2] drove them into the shallow epicontinental waters,

[1] It is presumed, but not proven, that these early hexactinellids were Lyssacine, that is, had the parenchymous tissue filled with detached spicules as contrasted to the fused parenchymalia of the Dictyonina.

[2] Austin H. Clark, writing of causes of marine migrations, says: "*Internal specific pressure* due to enormous increase in the number of individuals within a species operates not only to cause a species to colonize bathymetrically undesirable locations or unnaturally cold and uncongenial regions such as the polar seas but also to force species into small localized areas." (Quoted by Ruedemann, *Paleontology of Arrested Evolution*, p. 128, 1918.)

clothed in their new differentials. No shallowing of the sea or positive diastrophy is required for this explanation. By the time the Chemung outburst of species was effective all egress to or access from deep water was shut off. Examination of Schuchert's paleogeographic maps of this time will bring out this condition clearly. There was no deep-water Devonian in the vicinity at that period; to the east and south lay the Appalachian lands; to the north Laurentia, and on the west a long and, we must say, putative channel reaching in from the Pacific border. Through this channel the sponges may have gone out.

We conclude that the long evolution of these sponges from their appearance in the dark Cambrian and Ordovician muds to their immigration in the late Devonian was passed in the deeper waters of the continental edge and is recorded in sediments beyond the present reach of our observation.

Barrois discovered the Dictyosponges in the Psammites du Condroz of Jeumont in Brittany in sandy sediment at a horizon equivalent to the Chemung of New York, and four of these species in three genera were described and illustrated by Hall and Clarke (*op. cit.*). This is interesting collateral evidence of the widespread influence which in the Northern Hemisphere impelled these sponges on to the platform seas.

WHY AND WHERE DID THE CHEMUNG DICTYOSPONGES GO?

The course of their ontogenetic development shows that their later expression assumed gerontic and adaptive characters in great variety. The stratigraphic record indicates that the sandy bottom on which the New York colonies and their contemporaneous species grew was overwhelmed by incursions of coarse gravel washed in from the rivers of the eastern Appalachian land. These terminated their local existence and the Devonian period as well. Their emigration from southern New York was westward and into deeper waters of the Waverly group of western Pennsylvania and Ohio and the Keokuk lime muds of Indiana. In these Mississippian sediments they make their last appearance. But they were on their way down to deeper waters and we find no reason against the assumption that it was the westward course they followed on to

the epicontinental margin. As Dictyosponges they have never reappeared, nor as Lyssacine hexactinellids. That rôle was played. When their successors came back in the Jurassic and Cretaceous times their independent spicules had been fused into continuous networks and, as Dictyonine sponges, they carried on their important work as reef and rock builders. Seldom, however, did they reproduce the form of their Devonian predecessors; indeed the ancient form is far better revived in the glass sponges of today. That, too, is an interesting illustration of once more passing the same point on the cycle of their development history.

SUMMARY

1. In the Cambrian and Ordovician times the Lyssacine hexactinellids grew freely in the black muds of moderately deep epicontinental waters.

2. They were on their way off the American continental platform and down to the marginal seas.

3. Here they carried out their evolution during the long Silurian (when a stray species came ashore) and all the early stages of the Devonian.

4. In the later Devonian they return in great force and with their evolution fully under way, but not to such an extent as to conceal their ontogenetic stages and the radicle expression on which they were based. To this reappearance on the epicontinent they were evidently impelled by some *vis a tergo*, some compelling *external* force, probably the invasion of their province by a dominating life-element of another kind. They were caught in a general migration of the time into the shallow and cool waters of the Chemung, and in these waters they perfected their evolution.

5. Out of these shallow waters they were driven by an incursion of fresh waters which flooded the Devonian province with gravel from the eastern lands.

6. They migrated thence westward into the deeper waters of the Mississippian and from there once more to the circumcontinental seas.

7. In their return to the epicontinents of the Jurassic and Cretaceous their development had advanced to a change of skeletal structure and a wide variation of form.

8. Their departure from the Mesozoic epicontinents came with the opening of the Tertiary. They have never returned to epicontinental waters.

9. Today their descendants present a wide vertical range in the ocean waters, indeed an extraordinary adaptation through 2,800 fathoms. The deepest water forms are hopelessly isolated—they cannot climb the hill back to the zones of evolution and they will be as they are for future generations of observers. It looks as though all of them were traveling down to the depths; in which case the race will become stabilized and "immortal."

10. The history then is one of cycles of migration and development, of compelling impulses governing the former and probably inducing the latter.